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## *Cephalotus Follicularis: History and Evolution*

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### **Taxonomical data**

*Cephalotus follicularis* LABILL. is a taxonomically somewhat isolated species from S.W. Australia. Its closest relatives seem to be the Crassulaceae, a cosmopolitan family centered in Africa, and the Saxifragaceae, another widespread group originally from the North Pacific coasts (ENGLER). These taxa are now placed, together with the Cephalotaceae, in the Order Saxifragales (interesting data in SCHWEIGER, pp. 531-537; JAY & LEBRETON, p. 610; RAVEN & AXELROD, p. 586; JOHNSON, p. 38; CARLQUIST, 1981 p. 178).

The oldest fossils from the order Saxifragales date from the Upper Eocene (40 MYA) (MULLER, p. 52). Yet, for phytogeographical reasons, *Cephalotus*' ancestors are believed to have followed a tropical or subtropical migration route from Africa over Madagascar and India to Australia. In those days, during the Mid-Cretaceous (around 100-90 MYA) (RAVEN & AXELROD, p. 616) the Indian Ocean had not yet formed and the Dinosaurs still ruled the earth. Many other taxa used the same route. Later migrations (e.g. the ancestors of Australian *Drosera*) took the temperate route via Antarctica, which remained open until the Eocene.

### **The "normal" leaves:**

A few species in the Crassulaceae and Saxifragaceae have leaves resembling the "ordinary unaltered leaves" (GILBERT, p. 159; HAMILTON, p. 381) of *Cephalotus follicularis*, most strikingly *Saxifraga dungbooi*. Could this leaf type indeed be the precursor of the modern pitchers?

On closer examination, the foliage leaves do not appear to be so normal. In a classical two-sided (bifacial) leaf, a transverse section of the petiole shows the vascular bundles usually forming an arc, with the xylem situated adaxially. The same orientation is preserved in the nerves of the leaf/blade. But in the winter leaves of *Cephalotus* the bundles form a *ring*, and their xylem faces towards the axis of the petiole. Their position is but little modified in the lamina (MAURY, p. 165; MACFARLANE, 1911 p. 7; TROLL, 1932a p. 269 + pl. 80; ARBER, p. 569 + fig. 3; LLOYD, p. 82 + pl. 10-4). This circular arrangement of vascular tissues is typical of peltate or pitchered (epiascidiate) leaves, i.e. of laminae whose adaxial surface has become the inside of the pitcher, the abaxial surface forming the exterior (TROLL, 1932a with important modifications by ROTH, 1949 & 1952). The so-called normal leaves thus appear to possess a mixture of archaic characters (a bifacial lamina) and of more advanced ones ("unifacial" disposition of vascular bundles). They must therefore be inhomogenous, teratological structures (resulting from abnormal development).

## Teratological leaves:

This is the more interesting since *Cephalotus* is known to produce teratological leaves quite easily, both in culture (MASTERS, p. 314; DICKSON, 1887; HAMILTON, p. 38; SCHWEIGER, p. 498; TROLL, 1932a p. 268; HENNERN; KUSAKABE) and in the wild (HAMILTON, p. 38). These are intermediate in shape between the winter leaves and normal pitchers, and appear as inhomogeneous as the former. Some of them form almost complete pitchers, but the lid structure resembles that of the flat leaves, and what should have become the peristome is a ciliate rim. Others are flattened with almost no cavity, but the rim is rather well developed and looks like that of a normal lid. None of these mixtures of archaic and modern elements could actually represent the ancient trap.

The embryology of the *Cephalotus* leaves and traps has not yet been studied. A comparison with that of other peltate leaves (TKOLL, 1932a; ROTH, 1949 & 1952) leads to the following hypothetical model: the squat leaf initial (EICHLER, p. 194 & fig. 1) is bifacial. A ventral meristem forms on the flat adaxial face of the petiole. Cell proliferation causes the petiole to become cylindrical, i.e. round in transverse section instead of crescent-shaped as it was before. The older parts of the petiole contained a (bifacial) arc of vascular bundles. New ones form in the ventral tissues. They close the arc, which becomes a complete circle of bundles. Normally the distal part of the meristem produces a transverse ridge which will become the pitcher lid. Probably due to unfavourable conditions, this only happens to a variable extent in teratological leaves. The flat ones appear to possess no transverse parts at all. Yet I wonder if the ventral meristem does not produce at least some of the cells of the adaxial side of these leaves: firstly, the vascular bundles of the lamina keep their unifacial arrangement; secondly, the regressive leaves observed by Holger HENNERN (1987) could be considered as flat leaves with apical peltation. The distal cells of the ventral face, who decided to produce a transverse rim when the leaves were nearly finished, must have been derived from the ventral meristem also! Thirdly, the two faces of the flat leaves are histologically very similar (MACFARLANE, 1911 p. 7), i.e. of the same type as the exterior of the pitchers. TROLL (1932a p. 270) considered regressive leaves resembling the flat ones as an hypertrophy of the broadened upper part of the petiole (see sagittal section in MACFARLANE, 1911 p. 8 fig. 3A). As they are much smaller than normal pitchers, this part of the leaf is relatively much more prominent (see cover photograph of LECOUFLE, 1989!).

## Were early leaves peltate?

As we just saw, the common belief that the pitchers of *Cephalotus* evolved from flat leaves, such as the ones produced at the end of the winter, must be wrong. Then what did the archaic peltate leaf look like? This foliar shape exists in several species of the Crassulaceae (e.g. *Umbilicus Pendulinus* DC) (BERGER, p. 358) and of the Saxifragaceae (*Boykimia tellimoides* ENGL., *Chrysosplenium peltata* TURCZ., *Peltiphyllum peltatum* ENCL., the genus *Rodgersia* e.a.) (TROLL, 1932a p. 237). Kidney-shaped leaves frequently occur in the Saxifragaceae. They could easily have led to peltate forms. Related species in the same family show an easy evolution from entire to incised or divided leaves, and back (ENGLER, p.9).

Now the most common teratological pitchers in *Cephalotus* possess a strange lid with two pointed lobes which are remarkably leaf-like. Rarely, there is a smaller third lobe, which is attached to the midline, somewhere on the underside of the lid (DICKSON, 1887 p.174 & fig. 4). There would have been an easy embryological explanation for the presence of two lobes: the ventral meristem is often more developed laterally than on the midline! There is no similar hypothesis I can see for the presence of three lobes.

At the end of last century, the lid of the *Nepenthes* pitcher was thought to derive from the fusion of archaic folioles (secondary leaflets). This theory has been abandoned in the absence of confirmation from embryology or from the geometry of the lid's vascular system (see in LLOYD, p.60). But things lie differently here. The vascular supply of the *Cephalotus* lid has been shown to lack a median nerve. Each half of the operculum receives its own bundles (ARBER, p.569). From this and from the teratological data mentioned above, one may infer that the lid derives from the fusion of three leaflets, or of three lobes, depending upon whether the peltate leaf was only incised, or truly divided. The tissues and vascular supply of the insignificant median foliole cannot be traced in the modern operculum and in most regressive leaves. Yet the lid receives three main bundles (MAURY, p.164), with some variability due to anastomoses (ARBER, fig. 4,B & C1-2). There is also the occasional bundle crossing the midline, which in a way is a violation of the lid's bilateral symmetry.

Was the ancient leaf truly divided? The fact that the three-lobed regressive lids are not really trifold, but that their median lobe possesses its own attachment, seems to indicate that it was. In teratological leaves the lid is often as large as the pitcher. The ancestral leaf may therefore have been constituted of three about equally sized folioles, plus a smaller one.

What could have caused the evolution towards carnivory of ancestral plants with such leaves? The most archaic, and probably the least modified parts of the modern *Cephalotus* plant, i.e. the rhizome, underground scale leaves and the petioles are all covered with long hairs: but between these, numerous nectar glands can also be seen (DICKSON, 1881). Besides showing that the stem has not always been buried (why are glands there?), this confronts us with a paradox: why this mix of insect-repellent hairs and insect-attractive glands? Did the latter entice the insects to entangle themselves in the dense fur, to die there so that their decomposition products could be resorbed? But why then is carnivory not more frequent among hairy plants? There must be other factors in relation with the architecture of the leaf.

### **Folded unifacial leaves:**

TROLL (1932b) has described a phenomenon called 'diplophyly'. Picture a kidney- or arrowhead-shaped leaf. Imagine the parts of the lamina on both sides of the petiole to curl up towards the leaf apex. Now flatten this leaf and imagine a certain degree of fusion in the area where the lateral parts are folded. You have obtained a diplophyllous leaf, i.e. one with two large flaps growing out of the lamina. Now fold this leaf along the midrib in the manner of a *Dionaea* trap, and you get the shape of *Caltha dionaeaeifolia* (Ranunculaceae) (TROLL, 1932b p.193). This plant from Tierra del Fuego was once thought to be carnivorous (see *ibidem*, p.389). It is taxonomically rather close to *Cephalotus* (SCHWEIGER, p.534), so we are not comparing totally unrelated taxa here! The surfaces of the lamina, visible from the outside, are devoid of stomata. These are the more prominent on the adaxial surface of the leaf blade and on the side of the flaps which faces towards the same. Why plants should develop such leaves is still somewhat of a mystery. Could this be a protection against the desiccating wind? Tierra del Fuego is a very rainy region, and sailors of old dreaded the storms along its coasts. Another species with such leaves, *Alchemilla diplophylla* (Rosaceae, again close relatives of Cephalotaceae!) grows half submerged (*ibidem*, p.406). I wonder whether diplophyly could be an adaptation against the rain (or the current) bleaching minerals out of the leaves? *Caltha dionaeaeifolia* grows on sterile peaty substrate with carnivorous plants. It probably could not afford to lose minerals to raindrops swept on and off its leaves.

Now what do we know about *Cephalotus*' (sub)tropical ancestors? The modern plants never form root hairs. These are reduced to minute pimples, visible under the

microscope in juvenile roots (MACFARLANE. 1911 p.2). The leaves' epidermal cells have wavy cell walls (HAMILTON, p.44). In the Saxifragaceae this is typical of species living in wet habitats (ENGLER. pp.9-10). So *Cephalotus* must always have been a swamp plant. Then why the hairs? Their localization (petioles, margins and over the abaxial nerves) could mean that they evolved to bar access to the underside of the leaves. In the tropics, this is where insects usually dwell. out of sight of predators and sheltered from the rain. Were the hairs an adaptation to the dry season? *Cephalotus'* wood anatomy shows something similar: the simple perforation plates of the xylem vessels (CARLQUIST, 1981) is typical of xerophytes, and also found in most West Australian plants (CARLQUIST, 1976). But although I have not been able to check all species, the plants growing alongside *Cephalotus* do not appear to be so hairy. Or have the trichomes something to do with windswept environments such as drafty coastal swamps? A modified peltate structure resembling diplophyllous leaves would be as advantageous during the rainy season as it is to *Caltha dionaeaeifolia* in South America all year around.

This hypothesis appears to be very fertile. One may imagine the three folioles now forming the lid as laying very close to, and indeed almost covering the apical leaflet (which has become the pitcher cavity). The adaxial surface at the base of all these could have undergone a certain degree of fusion. This would explain the ease with which the cavity of teratological structures, most prominently the winter leaves. can become obliterated.

### **Adaptation towards carnivory: hairs.**

The evolution towards carnivory of such leaves becomes much easier to picture, too.

The idea that insects may find shelter between the leaf-lobes of *Caltha dionaeaeifolia* is an old one (HUTH. 1891). In this case nothing would prevent them from leaving afterwards. Things could have been different in the archaic *Cephalotus* leaves. To start with, ciliated rims are a frequent feature in the Crassulaceae (BERGER, p.359). That the rim of the ancient *Cephalotus* trap was ciliated is shown by the edges of the lid and pitcher of many regressive Leaves. In the original, flattened peltate trap the entrance would have been a narrow horizontal slit between the more or less fused lid folioles and the "pitcher" leaflet. Ciliae on both rims would have been effective in preventing egress if they were directed towards the inside. Their number would then increase and they would invade the pitcher inside, until they made up a broad band along all margins. As the apical leaflet transformed more and more into a pitcher, the trichome-covered walls tended to become vertical. So did the lid, and the opening of the trap became too wide to be closed off by cilia. The unicellular hairs then became shorter and shorter until they were reduced to the scaly cell processes now covering the underside of the lid, the peristome and the slippery funnel underneath.

A tight row of very short hairs is still found on the rim of the modern lid. Its aim probably is to seal the maturing pitchers, which are tightly closed. Since there are no transition forms between these short hairs and the scales in the inside of the lid (as I have ascertained), their homology with the latter remains dubious.

### **Translucent patches:**

These trichomes are very prominent on the lid of the juvenile type of pitchers, together with the well-known array of translucent areolae. The usefulness of these has been much debated. Since the operculum of mature pitchers is almost vertical (when the pitcher rests obliquely against the ground), the clear patches do not appear to be of much use. In pitchers of young rosettes the lid remains fairly horizontal. The windows serve a greater purpose there and appear relatively larger. In the archaic leaf

with its narrow entrance the areolae must have been even more useful. They may now be vestigial structures.

### **The peristome :**

One of Holger HENNERN's (1987) teratological leaves shows that in the past all the margins, including what is now the peristome, were of the same type, i.e. with alternating translucent areolae and coloured ridges. This confirms ARBER's 1941 hypothesis which said the ring-like structures of the modern peristome are homologous with the thickened ribs of the lid. The second HENNERN leaf may show how the normal peristome developed: by a process of folding in the manner of a mediaeval purse. The thin translucent parts became obliterated. Such a thickening of the leaf margin is no exception in the Saxifragaceae where undulated, knobby or toothed rims have been described. The marginal thickening does not entirely spare the *Cephalotus* lid. Its edge is clearly bloated where it meets the peristome. This can be very prominent in regressive leaves (see LLOYD, pl. 10-18), but scarcely sufficient to indicate that the lid results from the fusion of five instead of three folioles!

### **The flanges:**

Two pairs of well defined creases on the exterior of the pitcher (one on each side of the median flange) may also be remnants of this folding process. They probably contribute to the strength of the pitcher wall, a role also attributed to the ciliated flanges which are prominent features of this plant. These must be of considerable antiquity, as they are seldom lacking even on the most primitive regressive leaves. They are always situated over major vascular bundles, and must be homologous with the thickened nerves seen on the abaxial leafside in many taxa. The *Cephalotus* pitcher rests obliquely against the ground. It would tend to sag, forming a horizontal crease on its foreside, if it were not for the crests. The prominent ciliation shows these to be insect guides (not paths!). Their hairs also provide protection during the growth of the pitcher buds. The two faint ciliated ridges between the lid margins and the petiole have sometimes been considered as the rims of the adaxial side of the leaf (ARBER, p.569). Since this latter is unifacial, this cannot be true. These ridges could mark the site of fusion between the ciliated margins of folioles. They could also be folds of the basal, undivided part of the peltate leaf. The other lines of fusion between lid leaflets have vanished. Why then has this one been preserved? Maybe because its ciliae are useful in turning insects away from the lid where they would escape capture?

### **The origin of the glands:**

But all these structures would be useless without alluring and digestive glands. The presence of glands on all surfaces of the modern plant (and not only on the ones involved in carnivory) shows that they must derive from widespread elements. Possible candidates are: stomata, water-stomata, normal or glandular hairs. The small trichomes of the lid margin appear able to absorb safranin (HAMILTON, p.39). This seems insufficient to establish a relation with the glands. Unaltered stomata still exist on all external surfaces alongside the glands (DICKSON, 1881; MACFARLANE, 1911). Water-stomata are known in some Crassulaceae (BERGER, p.367) and in at least six genera of the family Saxifragaceae. Many of the latter's species live in humid or wet biotopes. The hydathodes do not only excrete water, but instances are known where the solution contains so much calcium salts that they accumulate on the leaves (ENGLER, pp.11 & 29). Hydathodes appear to be the best candidates in an ancient swamp dweller such as *Cephalotus*.

Some glands of the digestive patches of the pitcher inside look a lot like stomata (DICKSON, 1881), and these have now been shown to secrete enzymes (JUNIPER, ROBINS & JOEL, p.177).

The smallest glands of the peristome possess two surface cells which sometimes resemble stomata with a vestigial pore (SCHWEIGER, p.508 & figures 25-26; compare with PARKES & HALLAM, fig. 1-4 and JUNIPER et al., fig. 6.35).

The larger, fluid-producing glands of the pitcher cavity derive from these, even if they do not look like stomata. Connections of the largest among them, and of the peristome nectaries, with dead-end tracheids of the vascular system have sometimes been described (MAURY, p.166; HAMILTON, p.43; SCHWEIGER, p.509; PARKES & HALLAM, p.599; PARKES, 1980). This could be expected from modified hydathodes.

There are strange stalked glands in the flowers of *Cephalotus*. They also look remarkably stomata-like, but their stalk does not contain tracheids (DICKSON, 1881; MACFARLANE, 1893 p.445; SCHWEIGER, p.526). What these and the glands on the stem and petioles secrete is not known. I have checked HAMILTON's observation (p.50) that the latter indeed produce fluid which like the other secretions in *Cephalotus* does not seem to contain glucose. Gland cells are said to only give a faint histochemical reaction for glucose (EICHLER, p.497), maybe a cross reaction with another sugar?

How could the absorptive function, a prerequisite for carnivory, have appeared in such glands? According to MAURY (p.166), water-stomata are also able to absorb. They may have started by taking back salts bleached out of the plant by the rain, especially in the folded leaves, where the water could not run away quickly. To this would be added the minerals leaking out of dead insects, caught by the long hairs, maybe even before the special leaf shape was developed? The (simultaneous?) excretion of water and resorption of solutes by the same structure(s) is still obvious in the modern pitcher!

### Recent acquisitions:

Four recent features have completed the trap evolution as pictured here.

The peristome has produced a series of claw-like emergences. Small insects sipping nectar from the large nectar glands situated on these will fall straight into the pitcher fluid if they lose their grip (MACFARLANE, 1911 p.9; ADAMS & SMITH, p.271).

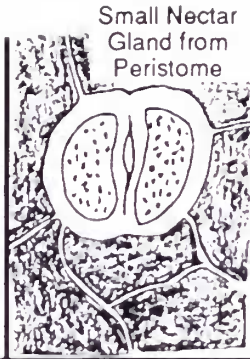
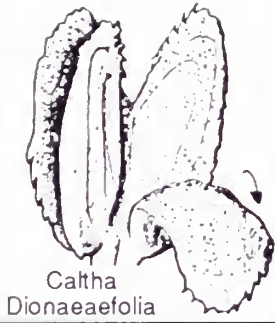
The slippery funnel has thickened and its lower rim forms an unscalable cornice. This structure appears rather late during the development of the leaf bud (HAMILTON, p.48) and must therefore be a recent acquisition.

The lid has become almost vertical and now presents some very prominent colour markings towards the outside. This may indicate that the plant is now also trying to attract flying preys, besides its usual victims, ants. In my terrarium almost all pitchers contain the dismembered remains of numerous small mosquito-like insects (and, fortunately for me, no ants).

Because of the large pitcher cavity, a greater volume of secretions is needed. This is provided by giant glands sunken in two thickened patches of wall. They are not yet noticeable in 2.5 mm buds (HAMILTON, p.45), so the same conclusion applies here as for the funnel.

### Acknowledgments

I wish to thank Holger HENNERN, who sent me two teratological leaves of an as yet undescribed type, and also Mr. Isamu KUSAKABE, who let me use his excellent photographs of regressive leaves.



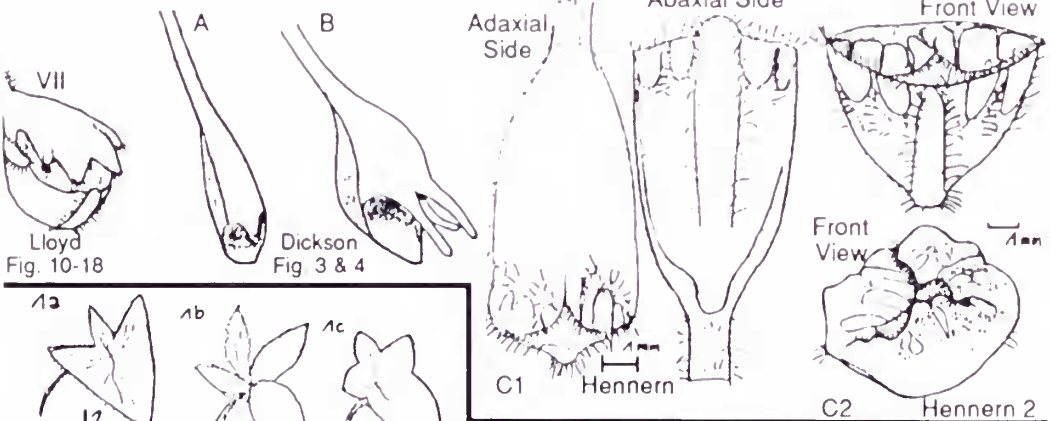
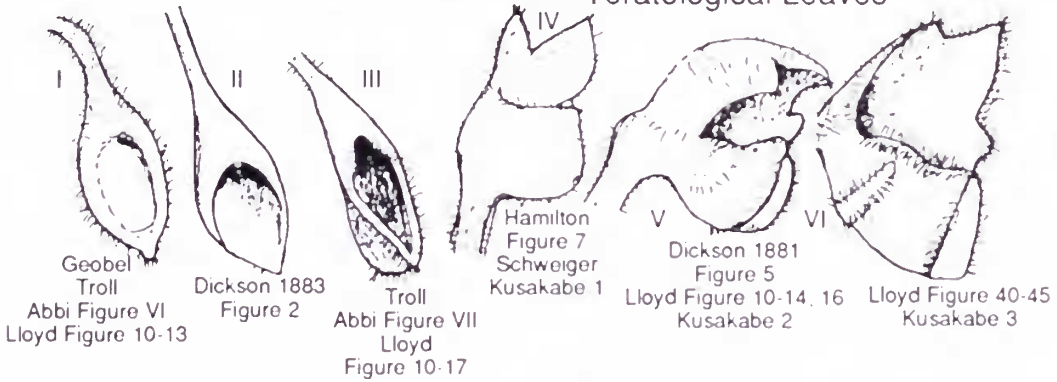
Caltha  
Dionaeaeifolia

Small Nectar  
Gland from  
Peristome

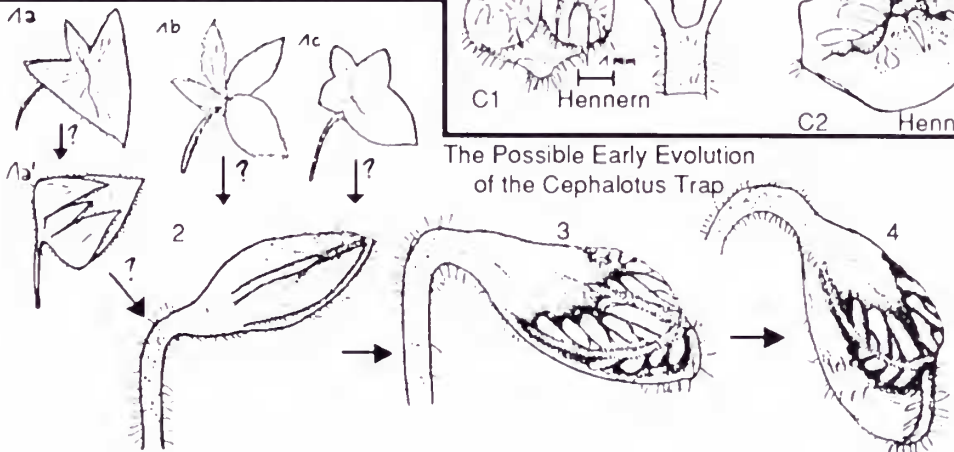
Small Digestive Gland  
from Coloured Patch

Stalked Gland  
from Flower

### Teratological Leaves



The Possible Early Evolution  
of the Cephalotus Trap



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## Grafting of *Nepenthes*

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During the last few years, many *Nepenthes* species have come into cultivation worldwide, some for the first time, even as their home ranges shrink under human development. As with any multi-species genus, there are species relatively easy to cultivate and those more elusive. The problems with difficult species can be as numerous as the plants themselves: temperature cycles, moisture levels, and one of the least understood parameters, simulating native soils or providing an appropriate alternative.

Transplanting species narrowly restricted to certain soils into an artificial media frequently results in poor growth, chlorosis (yellowing of the leaves), and eventual death. When such plants are removed from the media, few or no live. Roots are found or the root system is often extremely poor. Growth from seed in these mixes is also difficult with seedlings frequently never growing beyond the cotyledon stage.

If the native soils cannot be duplicated and roots will not survive in exotic media, grafting may be a reasonable alternative. Known from Biblical times, grafting was (and is) used to perpetuate a particularly fine species or cultivar, or to cope with nutritional, disease or pathogenic problems in a soil exotic, or even hostile, to the desired plant. The idea of grafting *Nepenthes* is not new and has been tried locally on several occasions. Most involved using an already established rootstock, and attempting to graft on a scion of the desired species. Invariably the host rejected this material, the reason not being entirely clear. This method should not be entirely rejected and is worthy of experimentation. As an alternate method, both rootstock and scion were taken as cuttings to form a whip graft. The rootstock consisted of two node lateral cuttings in which the dormant eyes were removed. The scion also consisted of a lateral cutting as opposed to a tip, the latter being more prone to rot under mist.

Ideally, the stem diameter of both scion and stock should be similar. A razor blade is used to shape the stems in the manner shown. (Figure 1) and after matching the cuttings the joint is wrapped tightly with plastic grafting tape. Not being self-adhesive